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METSCHNIKOFF ON GERM-LAYERS.<sup>1</sup>

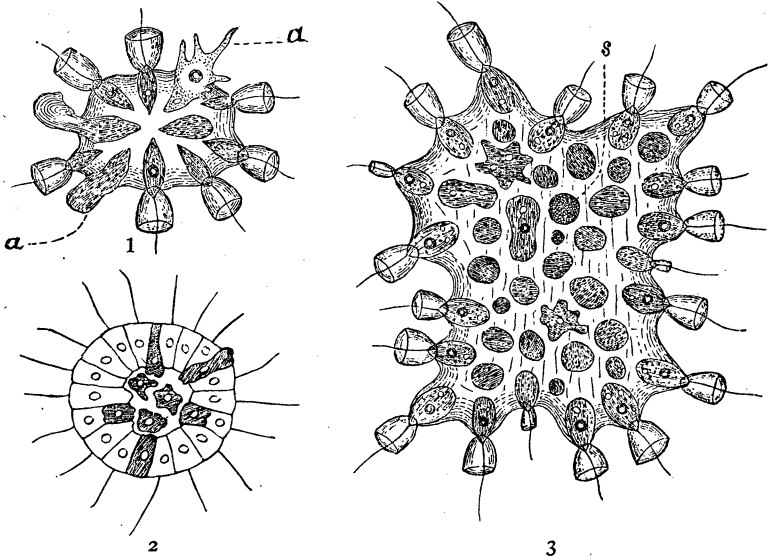
TRANSLATED BY H. V. WILSON.

(Concluded from page 350.)

IF we consider all that has been said on the theories in question, we cannot but see that they fail to establish the connection between the various embryological phenomena,—to combine them under one point of view, so to speak,—and that, moreover, they display a lack of physiological explanation. Some other theory must, then, be invented. In my studies on the Sponges (8) I very cautiously made a few remarks which, as I thought, agreed with what we knew of the way in which the endoderm was formed among the lower Metazoa, and which could be brought into harmony with the phenomena of intracellular digestion. I stated my belief that the endoderm did not appear in the beginning as a sac-like stomach with a terminal opening, such as one finds in the gastrula, but that behind these structures lay a long historic process, recorded in the formation of a solid parenchyma, in which digestion is intracellular. This parenchyma did not appear all at once, but was gradually formed from superficial blastoderm cells that migrated into the central cavity. There finally arose a two-layered parenchymella, which, by abbreviation of the embryonic process, along with the advancing differentiation of the digestive apparatus, became changed into a gastrula. At that time (1879) it was impossible for me to refer to any highly-developed Flagellate with animal nutrition. I therefore tried to find some foundation for my views in the development of *Volvox*, and in this connection made the following remark: "In my opinion it is time to begin looking for some low organisms in which the nutritive cells, perhaps after having taken in food, leave their usual position at the surface of the 'colony,' and come to lie within the central cavity" (p. 382). Shortly afterwards (July, 1880) Saville Kent discovered a most interesting form of Flagellate colony, which he introduced to science as *Protospongia h ckelii* (20). The individuals of a colony are at first regularly arranged at the surface. Some of these assume a pronounced am eboid shape, and migrate into the interior of the mass of

<sup>1</sup> The numbers in this article refer to the bibliographical list appended.

jelly, which serves to unite the members of a colony (Fig. 1, *a*). Here the amœboid individuals remain, to divide and suffer further changes, which Kent interprets as evidences of sporulation (Fig. 2, *s*). Whether the adoption of the amœboid form, together



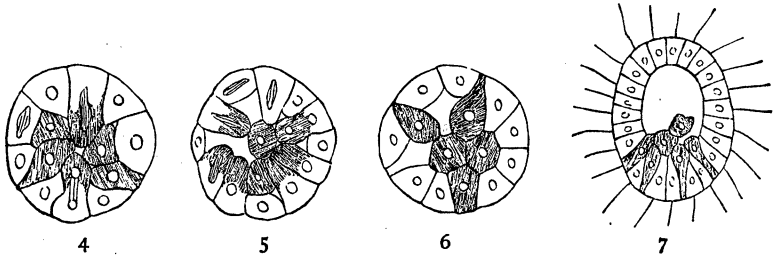
with the migration into the jelly, is in any way connected with the state of nutrition, cannot be asserted at present, since the phenomena involved are quite unknown. In view of the fact that the sporulation is as yet an open question, I hazard a guess whether the numerous granules seen by Kent be not either bits of indigestible stuff about to be cast out, or else particles of food just taken in. It would be extremely interesting to study more closely the genus *Protospongia* (also the second *Protospongia* form described by Oxley, and consisting of numerous individuals), paying special attention to the phenomena of nutrition and propagation. Meanwhile we may accept the fact that this Choano-Flagellate possesses two forms of individual, which naturally can pass one into the other,—a flagellate and an amœboid form, the latter of which is able to migrate from various points of the surface into the common mass of jelly. *Protospongia* thus offers such an unmistakable likeness to certain two-layered sponge-larvæ (for instance, the larva of *Aplysina sulphurea* de-

scribed by F. E. Schulze (33) ), that we may suppose the differentiation of an amœboid form of individual to have been the first step in the historic development of the endoderm.

At any rate, I believe the peculiarities of Protospongia can be more easily harmonized with my view (called by some writers the Parenchymella theory) than with any of the above-discussed theories of other investigators. But how does the Parenchymella theory agree with the facts of embryology in general, and of the Medusæ, as given in the preceding part of the book, in particular? In discussing this question we must, in the first place, recall the *a priori* conclusion to which I came regarding the multiplication of the hypothetical Metazoo-Flagellata. Reasoning from the fact that the first three segmentation planes (sagittal, frontal, and equatorial) in so many and various groups of animals follow the three dimensions of space, and consequently represent transverse and longitudinal division, I concluded that the ancestors of the Metazoa also possessed these two kinds of division. Gradually, however, the direction of division became more fixed, so that while one form divided exclusively or predominantly in a longitudinal plane another related form divided transversely. That such a condition of affairs as we have here sketched is not impossible is shown by the life-history of the several species of Salpingœca already referred to. We must therefore suppose that in our colonies of Metazoo-Flagellata certain of the superficial cells became amœboid and migrated into the centre of the colony, as occurs to-day in Protospongia, and that certain other cells divided transversely into two segments, one of which retained its position at the surface, while the other came to lie within the central space. Figure 3 illustrates these processes in a diagrammatic fashion. This double method of forming the endoderm, by the immigration of some cells and the cutting off of the central segments of others, is actually employed in those species that have a mixed delamination. For instance, *Polyxenia leucostyla* (Fig. 4). In the next place, transverse division became predominant in some forms (Fig. 5) and longitudinal division in others, in which latter case the endoderm was formed by the immigration of superficial cells (Fig. 6). In this manner mixed delamination split up into primary delamination, on the one hand, and multipolar immigration, on the other. Secondary delamination is to be regarded as a mere modification of mixed

delamination, from which it is distinguished by the late appearance of any difference between the ectoderm and endoderm cells.

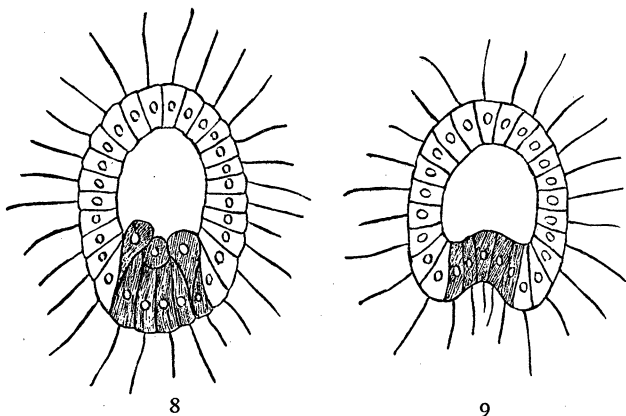
It is necessary to assume that multipolar immigration is a more primitive form than unipolar immigration (Fig. 7), since the contrary supposition leads us into great difficulties, as we have already seen. The transition from a multipolar to a unipolar immigration (where the seat of migration is always the hinder



end of the larva) is, on the other hand, an easy conception, especially as the latter is prone to occur in blastula larvæ that are very active, while the former is observed in motionless or sluggish embryos. It is as well to recall here the great predominance in the metagenetic Medusæ of cell-immigration over transverse division.

If there be no difficulty in deriving unipolar from multipolar immigration, there is likewise none in reducing invagination to the former. We learned in the third chapter that *Laodice cruciata* is distinguished from other metagenetic Craspedota by the fact that the posterior pole of the blastula is occupied by a continuous area of transparent cells. These cells, however, do not immigrate all at once, but one after another as in other Medusæ (Fig. 8). There is then formed a parenchymatous endoderm, which gradually acquires a cavity, the endoderm becoming epithelial. The stage with the area of transparent cells is strikingly like the blastula stage of *Nausithoë marginata*, Atlas, Plate X. (invaginate gastrula), in which the cells at the posterior pole likewise differ from the other cells of the body. Let us suppose the development of *Laodice* to be still further abbreviated. The endoderm cells, still at the surface but already differentiated, will no longer immigrate one at a time, but will invaginate in a body, and thus in a more direct way establish a gastric cavity (Fig. 9). The invagination of those cells that are

the first to differentiate, once accomplished, the neighboring parts of the blastoderm are also involved in the process, and the invaginated sac gradually becomes larger. The next stage in the process of abbreviation is not to be observed in the *Medusæ*. We may conceive it to consist in the still earlier differentiation of the endoderm cells, as a result of which all the cells destined to invaginate are already marked out in the blastula as peculiar elements. The flattened blastospheres found in *Lumbricus* and



the *Ascidians*, for instance, must be looked on as having been formed by some such abbreviation. In these blastospheres the ectoderm and endoderm areas are about equal. It needs no explanation to see that this early differentiation of the endoderm, carried far enough, will lead to the amphiblastula, will then make itself perceptible in the segmentation, and will finally be expressed in the structure of the egg itself.

It has been generally acknowledged since Kowalevsky's work on *Euaxes* that an amphigastrula (epibolic gastrula) may arise from an archigastrula by precocious differentiation. But it must also be admitted that a similar form (to the amphigastrula) may be derived from a mixed delamination by means of unequal segmentation. This latter view is supported by *Polyxenia leucostyla*. (The segmentation of this medusa is variable and in some eggs decidedly unequal, in which case the segmenting eggs strongly resemble epibolic gastrulæ.) It is thus evident that amphigastrulæ may come by two different ways from two different starting-points, and this embryonic form is hence polyphylitic.

From our point of view the endoderm must be regarded as an aggregate of cells, which were originally derived from the blastosphere by immigration or transverse division, and which then became associated together to form a mass of amœboid elements. The gastric cavity, as well as the mouth, must be regarded as later acquirements, whose appearance, however, in the ontogeny of certain forms has been so accelerated as to lead to the direct production of a gastrula.

Balfour (29), who has declared against the parenchymella theory, admits "that it fits in very well with the ontogeny of the lower Hydrozoa." Now that our knowledge of the facts is much greater than it was when this quotation was written, the harmony is still more marked. Balfour says in the same place (vol. ii, p. 285) that the passage from the protozoan to the metazoan state postulated by this theory strikes him as "very improbable in itself." But I cannot answer this criticism, since the assertion is made without any attempt to support it by argument. Much more precise are Bütschli's objections, which, however, concern the physiological side of the question exclusively. After a short account of my views, he remarks as follows (l. c., p. 418): "It seems to me that the endoderm cells, whose special business it is to take in food, would lose rather than gain by migrating into the interior of the colony. Without the simultaneous formation of a mouth, for which neither this nor Lankester's hypothesis can offer any reason, the immigration of the endoderm cells would be a decided disadvantage, since they then, so to speak, lock themselves in." When I first described my theory of the formation of endoderm by immigration (8), I referred to *Volvox*, in which the reproductive individuals leave the surface of the colony for the central cavity. At the present time I can also refer to the immigration of individuals that takes place in *Protospongia*, and which is certainly not without advantage to the colony in general. There are, moreover, *a priori* considerations to be taken into account. The individuals of a colony of *Flagellata* must first have become dissimilar, and this dissimilarity must then have given rise to a further differentiation. While some individuals were especially enabled to take in food, others were altered with reference to the locomotion of the colony and the attraction of food-particles. In motile colonies it must be of the greatest advantage

for the heaviest individuals, and consequently those laden with food, to move as near as possible to the centre. Another advantage would be gained if the nutritive persons were enabled to pursue their calling under the best possible circumstances. Now we know that many Flagellata pass from a monad into an amœboid stage, and it is especially in the latter that they feed. I will quote Bütschli's account (23): "In a large number of monads food is only taken in at a particular spot, which is almost always at the base of the flagellum. There is no doubt of this fact, and it is equally true, on the other hand, that certain of these forms, which have been observed to pass occasionally into the amœboid condition, are, during this condition, able to take in food at other points of the body." It is easily conceivable also that the nutritive individuals should multiply more rapidly than the others, and a connection might thus be established between an unusually large food-supply and multiplication. Still another cause for the occurrence of immigration is found when we consider that a colony could not increase its superficial area beyond certain limits. This fact must have exerted great influence on swimming colonies especially. Since increase in the number of individuals in our colony was sure to lead to increased activity, it was manifestly advantageous that cells, for which no room could be found at the surface, should adapt themselves to a life in the interior. The difference between individuals of the same stock was probably for a long time a mere quantitative difference: the locomotor cells attracted particles of food by means of the currents set up by their flagella, and also took in some of the smaller particles, as in certain Cœlenterates to-day, where the ectoderm cells occasionally take in bits of food (9). The amœboid individuals inside were, on the other hand, able to devour larger bodies, which the locomotor cells could not master. When thus engaged, the amœboid cells were very probably near the periphery, and no doubt made use of the numerous pores penetrating the superficial layer in order to get at the bits of food lying on the surface. For analogies to such a performance I may refer to the fact that in *Halisarca pontica*, under certain circumstances (8), foreign bodies are devoured by amœboid cells, and that in many of the lower animals the same is done by mesoderm cells. The differentiation gradually made greater progress in the path thus marked out. The locomotor



cells lost more or less completely the nutritive function, which became concentrated in the amœboid phagocytes. The very fine pores between the outer cells became larger, and formed mouth-openings similar to those so richly scattered over the surface of a sponge. As the colony more and more took upon itself the character of an individual (of the second order), the superficial persons (of the first order) became differentiated into an ectoderm or kynoblast, while the internal amœboid persons united to form a phagocystoblast (parenchyma or meso-endoderm). When the cells of the latter, acting independently, were not able to master unusually large particles of food, they formed a plasmodium, such as is often observed around large foreign bodies in the endoderm of Siphonophores or in the mesoderm of many animals. The metazoon, now provided with two primitive organs, steadily increased its activity, and in consequence the need of an abundant food-supply was likewise increased, so that it became necessary to prey upon vegetable and animal organisms of considerable size. To do this some entrance larger than that afforded by the pores was required, and one or more unusually wide openings arose, which ultimately led to the formation of a mouth.

The differentiation of originally uniform individuals into locomotor individuals and phagocytes finds many analogies in existing animals. In the lower Cœlenterates, such as Hydro-polyps, actinias, certain Medusæ (Oceania, Phialidium, Cunina), the entire endodermal lining of the gastrovascular system is able to feed upon bodies in the intracellular fashion. In consequence of this each endoderm cell is at once a phagocyte and a locomotor individual, in those cases at least where the endoderm cells are flagellate. In other Cœlenterates, for instance, in Aglaura among the Craspedota, in Siphonophores, and Cetenophores, the endoderm is differentiated into amœboid epithelium cells, which alone take in food-particles, and into flagellate epithelium cells, whose business it is to keep the current going, but which cannot take in foreign bodies. In the Sponges we find similar phenomena. In many representatives of this class the flagellate endoderm cells act also as phagocytes, while in some silicious sponges this latter rôle is exclusively in the hands of amœboid cells, the flagellate epithelium serving only to keep up the current of water.

It is evident enough that the migration of some individuals from the surface into the interior, which was probably filled with jelly, does not exclude the occurrence of transverse division in other individuals. It is also evident that the superficial portion of a cell which has thus divided might, when differentiation began, retain its original position, while the central portion lived on in the interior as a phagocyte.

The transitional form between the Metazoa and Flagellata has been called by me in a previous publication *Parenchymella*. I would like now to change the name to *Phagocytella*, for the reason that the latter suggests a very characteristic peculiarity of the form in question. The *Phagocytella*, as we have already learned, was characterized by the possession of two primitive organs, a kynoblast and a phagocytoblast, which were not as yet so sharply separated from each other as are the germinal layers of most Metazoa. Very probably the phagocytoblast continued for a long time to receive recruits from the kynoblast, in the shape of immigrating cells. As regards the development of *Phagocytella* we feel safe in supposing that the eggs (sexual multiplication must already have been acquired) underwent an equal segmentation, in which the divisions of the blastomeres followed the three dimensions of space; and that a blastocœl appeared very early, which was gradually filled up by immigrant cells and by the central portions of other cells that had suffered transverse division.

The *Phagocytella* theory is in harmony with our morphological and physiological knowledge of the Sponges. Indeed, it was in the study of this group that the theory had its origin. The embryology of the Sponges exhibits almost more variety than does the development of the Medusæ; at least, although far from being sufficiently studied, it reveals the several processes of immigration, delamination, and invagination. In general, then, what has been said for the Medusæ will describe the various ways in which the endoderm is formed among the Sponges. The primitive organs of the latter group, however, have progressed relatively but a short distance from their original state; it is for this reason that it is difficult to homologize the layers of a sponge with the germinal layers of other Metazoa. The "endoderm" often shades into the "mesoderm," the two structures being in the most intimate connection (8); I therefore think they

must be regarded as together forming a phagocytoblast. This conception is not in the least weakened by the fact that the cells forming these layers do not appear all at once, but often gradually migrate from the ectoderm (for instance, in *Halisarca*). The organization of the Sponges presents no peculiarities such as to justify us, along with Balfour and Bütschli, in separating the group from the other Metazoa. In this respect, therefore, I fully agree with most students of the Sponges, more especially with K. Heider (30). The lack of a mouth-opening, or in other words, the presence of numerous pores of entrance, can only be accounted as an important distinction, when an unwarranted genealogical significance is ascribed to these structures. From the stand-point occupied by the Phagocytella theory, these peculiarities of the sponge body are easily explicable. Again, the predominant part played by the amoeboid cells in taking in food would only give cause for surprise in case it were possible to speak of a differentiated mesoderm in the Sponges. But in this group there still endures a phagocytoblast, which must be regarded as the common foundation of endoderm and mesoderm; and consequently the rôle of the amoeboid cells presents no difficulties.

About a year after I had given in my "Studies on the Sponges"<sup>1</sup> a general sketch of my views, Balfour arrived at conclusions regarding the phylogeny of the Coelenterates which were in perfect accord with the principles of the Phagocytella theory. "Paradoxical as it may seem," says the English embryologist (29) (p. 147, vol. i.), "it appears to me not impossible that the Coelenterata may have had an ancestor in which a digestive tract was physiologically replaced by a solid mass of amoeboid cells. This ancestor was perhaps common to the Turbellarians also." It is very surprising that Balfour, believing this, was so strongly in favor of the gastræa theory, and regarded the parenchymella theory as improbable in itself. More recently Götte (34) has

<sup>1</sup> As early as 1877, in a paper on the digestive organs of fresh-water Turbellaria ("Memoirs of the Natural History Society of New Russia," vol. v.), I wrote as follows: "If the Turbellaria are actually parenchymatous animals, it is evident that in this respect there is a fundamental similarity between the lower representatives of two types of the Metazoa (Coelenterata and Vermes); that is, between Sponges and Turbellaria. If we compare the larvæ of the first group, particularly the *Amorphina* larvæ described by O. Schmidt, with the lower Turbellaria, we are at once impressed with the probability that these two classes are much more closely related than has hitherto been supposed."

published, without referring to Balfour or myself, a repetition of the view that a close relationship existed between the ancestors of the Coelenterates and Turbellaria (Acœla), and that the endoderm in the primitive Metazoa was in the shape of a parenchyma. From this paper it may be inferred that the number of students, who feel themselves compelled to postulate a Phagocytella-like condition, is gradually increasing. The latest researches on the anatomy of the Acœla (by Kleinenberg, Pereyaslawzew, Yves, Delage, and myself) confirm the statement of Graff, that a mesoderm and nervous system are wanting in these Turbellaria. The fact also remains that the digestive organs of the Acœla have preserved a very primitive condition, though it has recently been asserted that these worms possess an unmistakable digestive cavity.

On the contrary, the true Acœla exhibit an endodermal plasmodium containing vacuoles of various sizes, which may imitate the appearance of a special digestive cavity. I was best able to make out these facts on a transparent pelagic form of great beauty, which I obtained at Messina (where it has been several times studied by Kleinenberg), and which fully convinced me of the truth of the statement just made. It appears from the embryological investigations of Miss Pereyaslawzew (35) and of Repiachoff (36), that in the Acœla studied by them the segmentation is followed by a gastrula stage. The latter author concludes from this fact that the Acœla are degenerated worms. But the formation of a gastrula is by no means to be unconditionally regarded as a genealogically primitive process. In the development of the Medusæ we saw that the gastrula (in one case as the archigastrula of Nausithoë and Pelagia, in the other as the epibolic gastrula of *Polyxenia leucostyla*) might arise polyphyletically from totally different methods of forming the endoderm. It is quite possible, then, to regard the occurrence of a gastrula in the course of development as a secondarily acquired embryonic adaptation. Finally, I must remark that not until the work of Miss Pereyaslawzew and of Repiachoff has been published in full should an ultimate decision regarding the gastrula of the Acœla be expressed.

Since my view supposes that gastrula forms may arise independently in the course of embryonic development, on its adoption many difficulties encountered by the gastræa theory are

either solved or escaped. In this connection I refer to my "Studies in Comparative Embryology" (10), where I have discussed this side of the question. Blochmann (37) and Sedgwick (38) have recently endeavored to rescue the gastræa theory by once more propounding the view that the mouth and anus have both been formed from a slit-like blastopore. The evidence on which this view is based consists of Balfour's study of *Peripatus*, and of observations on *Aplysia* and other Gasteropods. The authors believe, however, that a slit-like blastopore which gives rise to both mouth and anus, may be assumed to occur in the Metazoa generally. But the gastræa theory is not thus freed of its main burden, for, if we accept this assumption, the radial gastrulæ of the Echinoderms, *Pilidium*, and *Polygordius* must be looked on as larval forms secondarily modified to a great degree, while the embryos of the Gasteropods, *Peripatus*, Insects, and Worms with a slit-like blastopore would represent the condition of the primitive gastrula. In like manner the regular blastospheres of the former animals would have to be regarded as the modified descendants of the amphiblastulæ, rich in yelk, of the latter.

The genealogy of the anus, which is not satisfactorily elucidated by the theory just discussed, is to be traced in a series of stages such as we have assumed to occur in the development of the mouth. In the lower Metazoa we observe two (*Ctenophora*) or more openings for the exit of the excreta, just as in the Sponges there are numerous openings for the entrance of food. In some of the Medusæ belonging to the family *Lafœidæ* (*Æquorea*, *Tima*) the numerous excretory openings of the gastro-vascular system are seated on special papillæ; some of the *Polycladæ* possess similar excretory openings on various parts of the body. In *Cycloporus* (39) Lang observed the extrusion of some drops of fluid containing differently-colored concretions through such external openings of the digestive apparatus. This observation is all the more significant because the *Polycladæ* possess, besides these openings, a special excretory system.

While one portion of the phagocytoblast developed into the endoderm, in which the originally amœboid cells gradually assumed an epithelial character, another portion of the same primitive organ gave rise to the mesoderm. The latter originally appeared in the shape of solitary migratory cells, which contin-

ued as before to function as phagocytes. This condition is found in many Coelenterates (where, however, in certain cases, additional cells migrate from the ectoderm, as in Corals, according to Kowalevsky and Marion), in Echinoderms, many Worms, etc. In some forms the whole mesoderm, in others only a part, permanently retained the original phagocytoblast condition. With many of the latter it came to pass that the mesoderm was formed by means of special sacs, which were constricted off from the endoderm. The cells of which these sacs were built ceased more or less completely to play the part of phagocytes. Such a condition appears in the Ambulacraria and in Vertebrates. In other animals with a simpler development,—for instance, Worms, Molluscs, and many Arthropods,—such mesoderm sacs have been looked for in vain; so that in these animals it is possible that the entire mesoderm has been derived from the original phagocytoblast without the aid of special endodermal sacs, though probably with some help from the ectoderm. In such cases the mesoderm has been able gradually to differentiate itself into a somatopleure and a splanchnopleure, without running through a sac-like stage. In Arthropods with a large amount of food-yolk the mesoderm is functional at a very early date, it being the habit of the mesoderm cells to devour the yolk-globules. Under such circumstances it can be understood how the mesoderm, even within the most recent time, has often been taken for the endoderm. In its origin dependent on the phagocytoblast, in part also on the kynoblast, the mesoderm sooner (Ctenophora) or later acquires its freedom and appears as a special germ-layer, which plays an important part in the development of the embryo. In opposition to the authors who think the mesoderm had its origin in sexual organs or muscles, I believe it was originally a part of the phagocytoblast, and as such took part in the inception or absorption of food. The importance of the mesodermal phagocytes in physiological and pathological processes, as well as the morphology of the mesoderm, have been discussed by me in other papers (7, 9, 10, 11, 12, 13), to which I may refer, and thus avoid repetition.

In conclusion, I wish to say that not until we are enlightened to the utmost as regards the primitive condition of the Metazoa will it be possible to place comparative morphology on a safe basis. But so long as the question of the germinal layers is

investigated in the anti-genealogical manner, all questions of greater importance will present the most invincible difficulties. For this reason I think that, in the absence of actual knowledge, hypotheses dealing with the early history of the germ-layers are not wholly unjustifiable.

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## HISTORY OF GARDEN VEGETABLES.

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(Continued from page 333.)

THE BEET. *Beta vulgaris*, var.  $\gamma$  L.

THE beet is essentially a modern vegetable. It is not noted by either Aristotle<sup>2</sup> or Theophrastus,<sup>3</sup> and although the root of the chard is referred to by Dioscorides and Galen,<sup>4</sup> yet the context indicates medicinal use. Neither Columella, Pliny, nor Palladius mention its culture, but Apicius,<sup>5</sup> in the third century, gives receipts for cooking the root of the Beta, and Athenæus,<sup>6</sup> in the second or third century, quotes Diphilus Siccineus as saying that the beet root was grateful to the taste and a better food than the cabbage. It is not mentioned by Albertus Magnus<sup>7</sup> in the thirteenth century, but the word *bete* occurs in English recipes for cooking in 1390.

Barbarus,<sup>8</sup> who died in 1493, speaks of the beet as having a

<sup>1</sup> Director of the New York Agricultural Experiment Station, Geneva.

<sup>2</sup> Aristotle, Scaliger's ed., 1566, 29.

<sup>3</sup> Theophrastus, Bodæus's ed., 1644, 778.

<sup>4</sup> Ex Fuchsius, De Stirp., 1542, 807.

<sup>5</sup> Apicius, lib. iii. c. 2, ii.

<sup>6</sup> Turre, Dryadum, etc., 1685, 443.

<sup>7</sup> Albertus Magnus, De Veg., Jessen's ed., 1867.

<sup>8</sup> Barbarus in Ruellius's Dioscorides, 1529, 124.